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**First boganiine beetle in mid-Cretaceous amber from northern Myanmar (Coleoptera:  
Boganiidae)**

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19 ABSTRACT

20 *Cretoboganium gei* gen. et sp. nov., a new amber inclusion of the cucujoid family Boganiidae is  
21 described and figured based on a well-preserved adult from the mid-Cretaceous Burmese amber  
22 (Hukawng Valley, northern Myanmar), some 99 million years ago. Based on the presence of a pair of  
23 pronotal callosities, *Cretoboganium* can be firmly placed in the extant subfamily Boganiinae, a small  
24 group currently comprising two small austral genera. Our discovery represents the first fossil record  
25 for Boganiinae. It also demonstrates another example that an apparently austral group may have its  
26 sister group occurred in today's northern hemisphere. Together with the other fossil boganiid known  
27 from the Middle Jurassic of China, the finding suggests that Boganiidae is an ancient and relict  
28 group. Moreover, the present biogeographic distribution of Boganiinae is indicative of an earlier  
29 origin of this subfamily, which likely originated before the breakup of the Gondwanan  
30 supercontinent.

31

32 **Keywords:**

33 Cucujoidea

34 Cenomanian

35 Burmese amber

36 Austral fauna

37 taxonomy

38

## 1. Introduction

With only 15 extant species placed in 6 extant genera, the cucujoid family Boganiidae is a small and distinctive beetle group, currently restricting to Australia, New Caledonia and southern Africa (Lawrence and Ślipiński, 2010; Escalona et al., 2015). All extant adults and larvae of Boganiidae seem to be pollenophagous. For example, *Boganium malleense* Escalona et al., belonging to the subfamily Boganiinae, occur in the flowers of *Eucalyptus gracilis* F. (Myrtaceae), and adults of *Athertonium* Crowson are collected in the blossoms of Myrtaceae, Elaeocarpaceae, Cunionaceae, Meliaceae and Lauraceae (Escalona et al., 2015). Although the phylogenetic relationships between Boganiidae and other cucujoid families remains unsettled, both morphological and molecular data indicate it as a member of the superfamily Cucujoidea (Lawrence et al., 2011; McKenna et al., 2015).

Fossil boganiids are very sparse. The first described fossil species, *Palaeoboganium jurassicum* Liu et al., is from the Middle Jurassic Daohugou beds (Inner Mongolia, northeastern China), some 165 million years old (Liu et al., 2018). *Palaeoboganium jurassicum* was suggested as a potential pollinator of Jurassic cycads based on phylogenetic evidence (Liu et al., 2018). As such, our knowledge about the early evolutionary history and historical biogeography of this small peculiar family is lacking. Here we reported the first amber-entombed boganiid beetle with exquisite morphological details preserved in the Cretaceous amber from northern Myanmar.

## 2. Material and Methods

The fossil species is described and figured based on a sole specimen preserved in Upper Cretaceous Burmese amber (Hukawng Valley, northern Myanmar; ca. 99 Ma). Observations and photographs were made using a Zeiss Discovery V20 stereo microscope and a Zeiss Axio Imager 2 light microscope with a digital camera attached respectively. The Zeiss Axio Imager 2 microscope was equipped with a mercury lamp and specific filters for DAPI, eGFP and rhodamine. Photomicrographs with a green background were taken under the eGFP mode, and those with a red

background were under the rhodamine mode. Extended depth of field images were digitally compiled using a Zerene Stacker v.1.0.4 software, and arranged in Adobe Photoshop CS5. The publication LSID is: urn:lsid:zoobank.org:pub:F9E63684-8BB6-40FE-AC61-D48C3FA3504F.

### 3. Systematic Palaeontology

Order: Coleoptera Linnaeus, 1758

Family: Boganiidae Sen Gupta and Crowson, 1966

Subfamily: Boganiinae Sen Gupta and Crowson, 1966

Genus: *Cretoboganium* gen. nov.

ZooBank LSID: urn:lsid:zoobank.org:act:4A3787D5-34FF-48A3-8485-700A7117593D.

Type species. *Cretoboganium gei* sp. nov.

*Diagnosis.* *Cretoboganium* can be readily distinguished from all known extant and extinct genera of Boganiidae by the following combination of characters: frontoclypeal suture strongly curved (possible apomorphy); clypeal base not constricted; antennae short, with distinct 3-segmented antennal club; maxillary palp short; pronotum with a pair of large callosities; prosternal process distinctly dilated at apex; and elytra with regular puncture rows.

*Etymology.* Combination of the Latin word *creta*, meaning chalk, and the generic name *Boganium*; it is neuter in gender.

*Description.* Body (Fig. 1) comparatively large for Boganiidae (ca. 3 mm long), elongate, slightly flattened, subglabrous.

Head (Fig. 2A) strongly transverse, not declined. Occipital region without transverse ridge.

89 Frontal region without median endocarina. Eyes (Fig. 2B) large, entire, strongly laterally  
90 protuberant, coarsely faceted, without interfacetal hairs. Antennal insertions (Fig. 2B) slightly  
91 concealed from above. Frontoclypeal suture distinctly impressed, curved; base of clypeus not  
92 impressed laterally, its anterior edge rounded, without teeth. Labrum concealed beneath clypeus.  
93 Antennae (Fig. 2B) with eleven antennomeres, with distinct, 3-segmented club (Fig. 3D). Mandible  
94 small. Maxilla (Fig. 2C) with setose galea; maxillary palp short.

95 Pronotum (Fig. 2A) setose, strongly transverse, about 0.65 times as long as wide, widest slightly  
96 before middle; sides strongly curved, not explanate; lateral pronotal carinae complete, simple, visible  
97 for their entire lengths from above, with raised margin; anterior angles rounded, with prominent  
98 callosities containing gland openings (Fig. 2B); posterior angles sharp and distinct; posterior edge  
99 weakly bisinuate, well margined; pronotal disc without sublateral carinae. Prosternum (Fig. 2C) in  
100 front of coxae slightly longer than shortest diameter of procoxal cavity. Prosternal process (Fig. 2C)  
101 complete, distinctly expanded apically; apex nearly truncate. Protrochantins exposed. Procoxal  
102 cavities strongly transverse, narrowly separated, externally broadly open. Scutellar shield not  
103 abruptly elevated, anteriorly simple, laterally expanded and rounded, posteriorly broadly rounded.

104 Elytra (Fig. 2D) about 1.6 times as long as wide and 2.9 times as long as pronotum, finely  
105 setose, with several indistinct rows of small punctures. Elytral apices meeting at the suture.  
106 Mesocoxal cavities moderately separated, subcircular. Metacoxae narrowly separated, not extending  
107 laterally to meet elytra. Hind wing, if present, not visible. Trochanterofemoral joint strongly oblique;  
108 tibial apices gradually widened at apex; tarsal formula 5-5-5 (Fig. 3A–C); penultimate tarsomere  
109 distinctly reduced and one preceding tarsomere lobed beneath (Fig. 3A–C); pretarsal claws usually  
110 simple.

111 Abdomen with five free ventrites; intercoxal process acute.

112

113 *Cretoboganium gei* sp. nov. (Figs. 1–4)

114 ZooBank LSID: urn:lsid:zoobank.org:act:6C581C66-8FDD-49AC-8A1F-DD937B0EA407.

115

116 *Etymology.* In honor of Mr. Chang Ge for his effort in sharing knowledge of Burmese amber and  
117 donating the holotype for our study.

118

119 *Material.* Holotype, NIGP167701, sex undetermined; deposited in the Nanjing Institute of Geology  
120 and Palaeontology, Chinese Academy of Sciences, Nanjing, China. Mid-Cretaceous amber (earliest  
121 Cenomanian or late Albian; Ross et al., 2010; Shi et al., 2012), Hukawng Valley in Tanai, Kachin  
122 State, northern Myanmar.

123

124 *Diagnosis.* Body relatively large (ca. 3 mm long), black; antenna short; and pronotal callosities very  
125 large.

126

127 *Description.* Body 3.09 mm long (measured from anterior margin of head to abdominal apex); black  
128 throughout the body.

129       Head strongly transverse; head surface glabrous. 0.44 mm long and 0.79 mm wide (across  
130 eyes). Eye large. Mandible small, not visible from above, apparently without teeth. Anterior margin  
131 of clypeus with dense anteriorly-directed setae. Antenna short, nearly asymmetric, with apical three  
132 antennomeres forming a distinct club; surface of antennomeres densely setose; antennomere 1  
133 elongate and broad, antennomere 2 subquadrate, narrower than antennomere 1, antennomere 3 longer  
134 than wide, antennomeres 4–8 almost in the same length and width, antennomere 9 nearly twice as  
135 long as antennomere 8, antennomere 10 in the same width and shape as antennomere 9, antennomere  
136 11 subconical, slightly narrower than antennomere 10. Maxillary palp short, palpomere 2 elongate,  
137 palpomere 3 very short, palpomere 4 fusiform, much longer than palpomere 3.

138       Pronotum strongly transverse, 0.68 mm long and 1.05 mm wide. Surface without punctures or

139 setae. Pronotal callosities located near the anterior pronotal angles, prominent from above. Apex of  
140 prosternal process dilated apically, with dense posteriorly-directed setae. Elytra complete, 2.0 mm  
141 long and each 0.64 mm wide, with regularly arranged rows of small punctures. Humeral callus well  
142 developed. Legs moderately long; tibiae setose, expanded at apex, apical tibial edges fringed with  
143 spines; tarsomeres 1–3 successively shortened, tarsomere 4 much shorter and smaller than the rest,  
144 tarsomere 5 long, as long as tarsomeres 2–4 combined; ventral side of pro- and mesotarsomeres 1–3  
145 covered with dense setae. Pretarsal claws long, curved. Genitalia not visible.

146

#### 147 **4. Discussion**

148 The new genus *Cretoboganium* can be confidently attributed to the extant cucujoid family  
149 Boganiidae based on the following combination of morphological features: 1) head with distinct  
150 frontoclypeal suture; 2) protrochantins well developed; 3) all coxae narrowly separated; 4) tarsi 5-  
151 segmented, with tarsomere 4 reduced; and 5) abdomen with five ventrites (Lawrence and Ślipiński,  
152 2010; Escalona et al., 2015). Another important diagnostic character for modern Boganiidae,  
153 mandible with dorsal setose cavity, is unfortunately not visible from the holotype. Moreover,  
154 *Cretoboganium* can be referred to the extant subfamily Boganiinae as strongly evidenced by the  
155 presence of paired pronotal callosities and the comparatively short and somewhat fusiform apical  
156 maxillary palpomere (Escalona et al., 2015). The subfamily Boganiinae currently comprises only two  
157 extant genera: *Afroboganium* Endrödy-Younga & Crowson (South Africa and Namibia) and  
158 *Boganium* Sen Gupta & Crowson (South Australia, Victoria, Tasmania and southeastern Western  
159 Australia) (Escalona et al., 2015). *Cretoboganium* can be easily recognized from these extant genera  
160 by a strongly curved frontoclypeal suture, striate elytra, compact antennae with an abrupt antennal  
161 club, and very large pronotal callosities.

162 The most distinctive feature of *Cretoboganium* is the strongly curved frontoclypeal suture. The  
163 frontoclypeal suture of modern boganiid beetles are all straight or nearly so (Lawrence and Ślipiński,



2010; Escalona et al., 2015). To our knowledge, a strongly curved frontoclypeal suture in Boganiidae is confined to two extinct genera: *Cretoboganium* presented here and *Palaeoboganium* Liu et al. from the Middle Jurassic Daohugou beds (Liu et al., 2018). As in the Jurassic *Palaeoboganium*, the clypeal base of *Cretoboganium* is not constricted at base, a character also found in one of the two extant genera: *Afroboganium*. By contrast, the clypeal base of the Australian *Boganium* is more deeply constricted (Escalona et al., 2015). Although *Cretoboganium* shares with the older *Palaeoboganium* the curved frontoclypeal suture and unconstricted clypeal base, *Cretoboganium* differs significantly from the latter by having strongly clubbed antennae, well-developed pronotal callosities, and much smaller body size (11 mm long in *Palaeoboganium* v.s. 3 mm long in *Cretoboganium*).

Another interesting character of *Cretoboganium* is the striate and finely setose elytra. Among all extant Boganiidae, this character is absent in the subfamily Boganiinae, but it can be found in one of three genera of the other subfamily Paracucujinae, i.e., *Metacucujus* Endrödy-Younga and Crowson. The paracucujine genus *Paracucujus* Sen Gupta and Crowson also bears regularly striate elytra, but the elytra lack fine setae (Escalona et al., 2015). The Jurassic *Palaeoboganium*, as a sister group to *Paracucujus* + *Metacucujus*, appears to have glabrous and regularly striate elytra (Liu et al., 2018).

The discovery of *Cretoboganium* from the mid-Cretaceous Burmese amber (approximately 99 million years ago) stands for the first fossil member of the extant austral subfamily Boganiinae. Such an old and comparatively precise age of this clade is of great importance for further phylogenetic analysis and divergence time estimation in future. This discovery represents another example that current southern hemisphere endemic group may have its sister group apparently occurred in what is now the northern hemisphere (e.g., Thayer et al., 2012; Cai et al., 2012; Krishna et al., 2013; Cai and Huang, 2017a, b). There is high-resolution aeromagnetic data indicating that the eventual breakup (formation of first true ocean floor) between the Antarctic Peninsula and southernmost South America occurred at about 147 Ma (König and Jokat, 2006). This happened before the separations

between Africa and South America, and between Antarctic and Australia (Jokat et al., 2003; König and Jokat, 2006). Therefore, it is very likely that Boganiinae first originated before the breakup of the Gondwanan supercontinent, at least about 147 million years ago. The previous find of a mid-Jurassic boganiid species from northeastern China (Liu et al., 2018) indicated Boganiidae as a very ancient group of Cucujoidea (Labandeira, 2000), and it was much more widespread in the Jurassic. Although there are no fossil boganiids documented from the Mesozoic of the southern hemisphere, we can expect such discoveries from the fossil deposits in the Gondwanan landmasses, such as the Late Jurassic of Australia (Talbragar fish beds; Cai et al., 2013; Ashman et al., 2015) and/or the Early Cretaceous of Brazil in the future.

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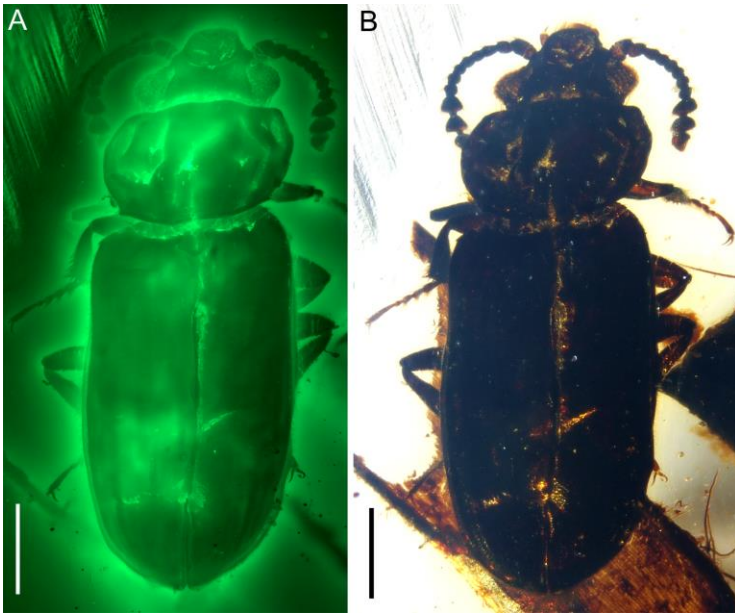
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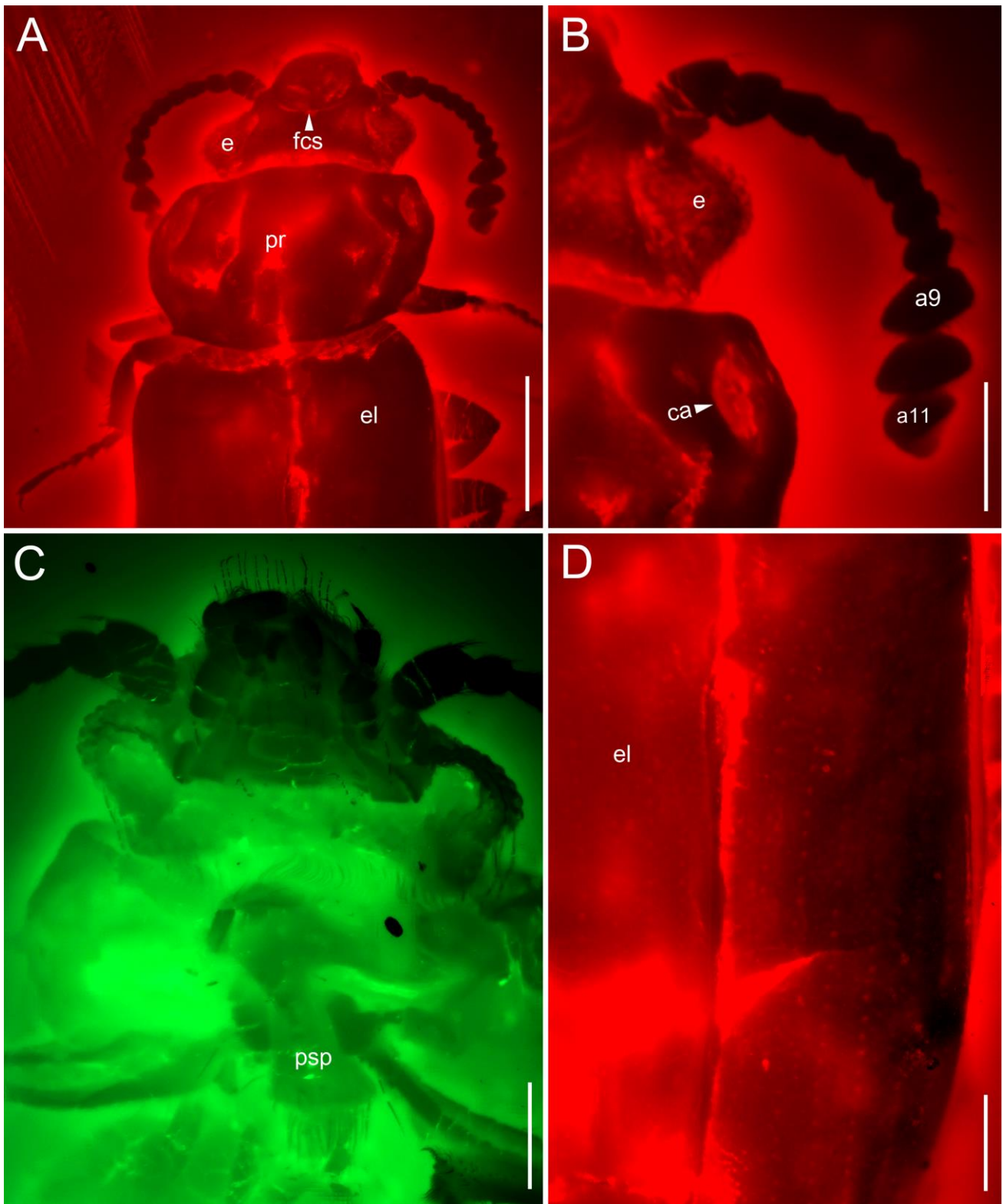
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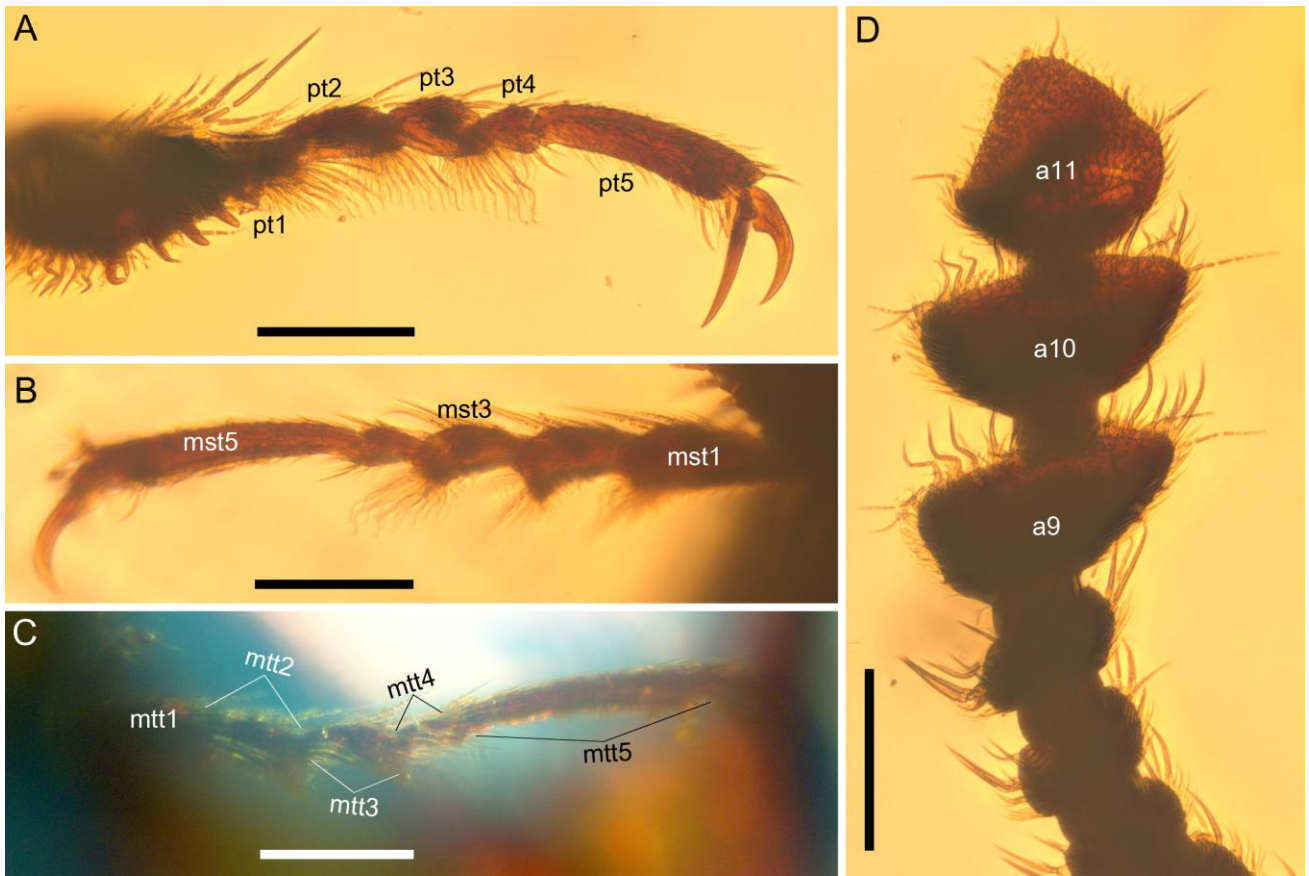
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**Fig. 1.** Microphotographs of holotype (NIGP167701) of *Cretoboganium gei* gen. et sp. nov. from Upper Cretaceous Burmese amber. A. dorsal view, under green fluorescence; B. dorsal view, under normal reflected light. Scale bars: 500  $\mu$ m.



**Fig. 2.** Enlargements of holotype (NIGP167701) of *Cretoboganium gei* gen. et sp. nov., under fluorescence. A. dorsal view of head, pronotum and partial elytra; B. enlargement of A, showing details of eye, antenna and pronotal callosity; C. ventral view of head and prothorax; D. dorsal view of elytra, showing regular puncture rows. Abbreviations: a, antennomere; ca, callosity; e, eye; el,

270 elytron; fcs, frontoclypeal suture; pr, pronotum; psp, prosternal process. Scale bars: 500  $\mu$ m in A, 200  
271  $\mu$ m in others.



272  
273 **Fig. 3.** Enlargements of holotype (NIGP167701) of *Cretoboganium gei* gen. et sp. nov., under  
274 transmitted light. A–C. pro-, meso- and metatarsus, showing reduced tarsomere 4; D. apical six  
275 antennomeres of right antenna, showing strongly clubbed antenna. Abbreviations: a, antennomere;  
276 mst, mesotarsomere; mtt, metatarsomere; pt, protarsomere. Scale bars: 100  $\mu$ m.





277

278 **Fig. 4.** Dorsal reconstruction of *Cretoboganium gei* gen. et sp. nov.